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# Local habitat composition and complexity outweigh seascape effects on fish distributions across a tropical seascape

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## Abstract

**Context** The distribution of animals is influenced by a complex interplay of landscape, environmental, habitat, and anthropogenic factors. While the effects of each of these forces on fish assemblages have been studied in isolation, the implications of their combined influence within a seascape remain equivocal.

**Objectives** We assessed the importance of local habitat composition, seascape configuration, and environmental conditions for determining the abundance, diversity, and functional composition of fish assemblages across a tropical seascape.

**Methods** We quantified fish abundance in coral, macroalgal, mangrove, and sand habitats throughout the Dampier Archipelago, Western Australia. A

full-subsets modelling approach was used that incorporated data from benthic habitat maps, a hydrodynamic model, in situ measures of habitat composition, and remotely sensed environmental data to evaluate the relative influence of biophysical drivers on fish assemblages.

**Results** Measures of habitat complexity were the strongest predictors of fish abundance, diversity, and assemblage composition in coral and macroalgal habitats, with seascape effects playing a secondary role for some functional groups. Proximity to potential nursery habitats appeared to have minimal influence on coral reef fish assemblages. Consequently, coral, macroalgal, and mangrove habitats contained distinct

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fish assemblages that contributed to the overall diversity of fish within the seascape.

**Conclusions** Our findings underscore the importance of structural complexity for supporting diverse and abundant fish populations and suggest that the value of structural connectivity between habitats depends on local environmental context. Our results support management approaches that prioritise the preservation of habitat complexity, and that incorporate the full range of habitats comprising tropical seascapes.

**Keywords** Fish · Habitat complexity · Seascape configuration · Environmental context · Functional group

## Introduction

Understanding the factors governing the distribution of organisms is fundamental to developing ecologically sound and locally relevant conservation strategies (Pullin 2002; Marshall et al. 2014; Villero et al. 2017). Yet, climate change and human activities are altering the composition and connectivity of habitats upon which many animals rely (Haddad et al. 2015; Hughes et al. 2018; Gissi et al. 2021). In tropical seascapes, this modification can impair ecosystem functioning, impacting the delivery of ecosystem services upon which millions of people depend (Moberg and Folke 1999; Boyd and Banzhaf 2007; Woodhead et al. 2019). Ecosystem functioning within seascapes is regulated by the flow of energy and materials through various ecological processes, many of which are performed by specific functional groups of fish (e.g. grazers, piscivores, and excavators (Odum and Odum 1955; Olds et al. 2012b; Brandl et al. 2019). Variation in the diversity, abundance, and composition of fish assemblages may therefore affect the delivery of important ecological processes across seascapes (Bellwood and Fulton 2008; Olds et al. 2012b; Harborne et al. 2016).

Fish assemblages in coastal seascapes are frequently subject to a broad range of co-occurring physical and biological drivers that can interact in complex ways (Boström et al. 2011; Ceccarelli et al. 2023). The effects of habitat composition and complexity (e.g. Graham and Nash 2013; Darling et al. 2017), seascape configuration (e.g. Grober-Dunsmore

et al. 2008; Nagelkerken et al. 2017), environmental conditions (e.g. Fulton et al. 2005; Moustaka et al. 2018), and fishing pressure (e.g. Dulvy et al. 2004; Graham et al. 2017) on fish assemblages are generally well understood in isolation (see *ESM Table 1* for a detailed summary); however, few studies investigate the implications of multiple forces acting concurrently within an individual system (Wilson et al. 2008; Olds et al. 2012a; Gilby et al. 2016; Sievers et al. 2020). Determining the relative importance of these co-occurring biophysical drivers, and how this may differ between important functional groups, is important for conservation planning (Harborne et al. 2017; Pickens et al. 2021). Of the studies that have assessed multiple drivers, all noted the influence of seascape configuration on at least one component of the fish assemblage (Gilby et al. 2016; Henderson et al. 2017; van Lier et al. 2018; Berkström et al. 2020; Sievers et al. 2020). However, there was little consensus as to the relative importance of seascape effects compared to other factors. This ambiguity may stem, in part, from the different habitats and environmental settings in which these studies were conducted.

Tropical coastal seascapes often exist as patch mosaics of coral, seagrass, macroalgal, mangrove, sand, rubble, and pavement habitats that are biologically and hydrologically connected (Sheaves et al. 2015). These different habitats contain distinct assemblages and/or life history stages of fish and contribute uniquely to the total diversity and functioning of the seascape (Harborne et al. 2008; Sambrook et al. 2019; Harper et al. 2022; Dunne et al. 2023). Moreover, some fish species exploit multiple habitats within the seascape on a diel basis to forage or shelter, sustaining important ecological processes across habitat boundaries (Luo et al. 2009; Hyndes et al. 2014; Vaslet et al. 2015). Consequently, holistic seascape management necessitates expanding our understanding of the factors structuring fish assemblages to encompass the range of habitats that comprise coastal seascapes.

Habitats within coastal seascapes are subject to dissimilar physio-chemical conditions (e.g. salinity, turbidity, and wave exposure) due to factors such as topography, prevailing winds, and freshwater inputs (Young 1989; Serafy et al. 2003). Fish assemblages in disparate habitat types likely respond differently to prevailing environmental conditions due to the species-specific tolerances (e.g. osmoregulatory

capacity) and characteristics (e.g. mobility) of the taxa present in each biotope (Denny 1994; Serafy et al. 1997; Sheaves 1998). Moreover, the disparate composition and complexity of benthic habitats represents a distinct range of resources and shelter, which can mediate the effects of environmental, anthropogenic, and biological influences (Brown et al. 2017). For example, intertidal mangroves are often physiochemically extreme and temporally variable environments (Igulu et al. 2014; Dubuc et al. 2019). As such, fish occupying these habitats may be most strongly influenced by seascape configuration because they must find alternative shelter at low tide (Pittman et al. 2007; Faunce and Layman 2009). In contrast, fish inhabiting fringing coral reef habitats may be subject to greater wave energy and predation pressure (Shulman 1985; Young 1989). In such environments, substrate complexity and the availability of suitable micro-habitat refugia may exert the strongest influence on the distribution of small-bodied species (Beukers and Jones 1998; Depczynski and Bellwood 2005). Uncertainty surrounding the relative importance of factors governing species distributions within and across tropical seascape habitats impedes our understanding of the functioning of these ecosystems.

Identifying the degree to which different biophysical factors influence the distribution of key functional groups of fish, and therefore likely the delivery of crucial ecological processes, and understanding how this varies among different habitats within a seascape, is important for effective management. To date, few studies have attempted to address this knowledge gap. As such, this study aimed to address the following questions: (a) what is the relative importance of local habitat composition, seascape configuration, environmental conditions, and human use in structuring the abundance, diversity, and functional composition of fish assemblages? And (b) how does the importance of these factors vary among different habitat types within a tropical seascape? The Dampier Archipelago in north-western Australia represents an ideal model system to investigate these questions as it contains numerous bays encompassing habitat mosaics with varying combinations and configurations of coral, macroalgal, mangrove, seagrass, and sand/rubble habitats (Morrison 2004). These bays are embedded within a complex oceanographic system that

generates cross-shelf gradients in environmental conditions (e.g. turbidity) over a relatively small spatial scale (Pearce et al. 2003; Moustaka et al. 2019).

## Methods

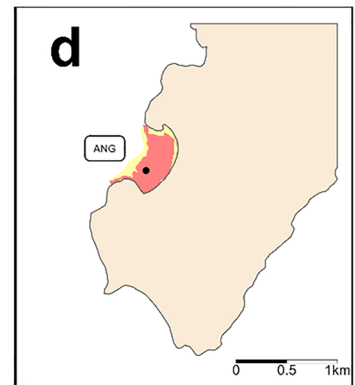
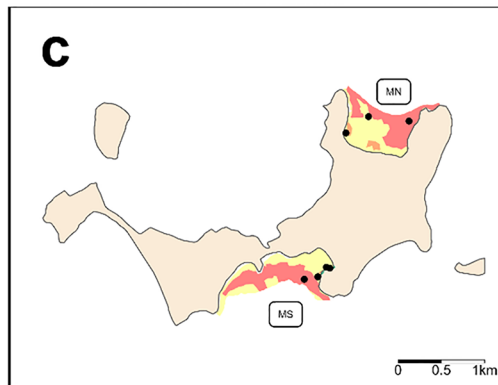
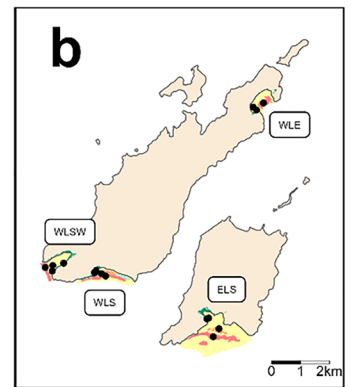
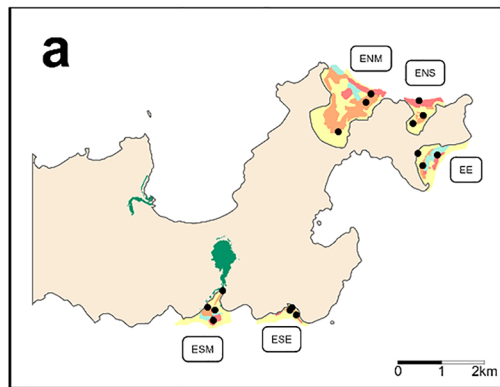
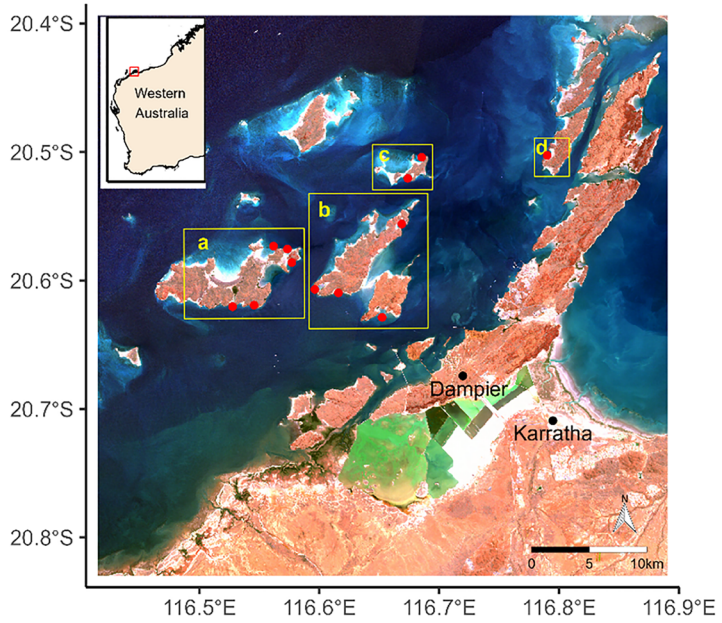
### Study location

The Dampier Archipelago comprises 42 islands fringed by variable habitat mosaics (Fig. 1; Morrison 2004). The region is macrotidal and experiences semidiurnal tides with a maximum spring tidal range of 5 m, resulting in extensive subaerial exposure of intertidal areas (Pearce et al. 2003). Tidal water movement, combined with wind- and wave-driven sediment resuspension, generates a strong and highly variable cross-shelf turbidity gradient with anomalous spikes caused by natural and anthropogenic disturbances (Blakeway et al. 2013; Moustaka et al. 2018; Evans et al. 2020). The archipelago has been subject to significant modification, including the construction of Australia's largest tonnage port, regular dredging of shipping channels, and ongoing vessel traffic (WAEPA 2007). The archipelago is also subject to moderate levels of recreational boat usage and fishing managed by bag and size limits at the regional level. While there are currently no spatial (e.g. marine protected areas) or temporal (e.g. seasonal closures) restrictions on recreational fishing, the Dampier Archipelago has historically been recognised as a site of conservation value and recommended as a potential marine protected area (CALM 1994). Commercial fishing effort within the Dampier Archipelago is minimal as the major demersal scalefish fisheries (trap and trawl) are restricted to offshore waters (Newman et al. 2023). Twelve shallow (< 7 m depth) bays of similar size were selected as study sites based on the presence of substantial structurally complex habitat (i.e. coral, macroalgae, mangrove) and spatial distribution.

### Habitat mapping

Satellite imagery (Sentinel-2, 10 m resolution) paired with georeferenced ground-truthing habitat data collected from 2020 to 2022 were used to manually digitise marine benthic habitats using ArcMap 10.8.1

**Fig. 1** Location of the twelve study sites throughout the Dampier Archipelago, Western Australia, and associated benthic habitat maps to the 7 m depth contour (see ESM Fig. 2 for large versions of maps). Black dots indicate the locations of fish/benthic sites (3 × 30 m transects per habitat type) surveyed in January 2021



Habitat ■ Coral ■ Macroalgae ■ Mangrove ■ Mixed Coral/Macroalgae ■ Sand

(ESRI 2020). Habitat classification was limited to depths of less than 7 m (relative to mean sea level) to ensure sufficient clarity to identify benthic features. A simplified four-category habitat classification scheme was used, which included sand/rubble/bare substrate (hereafter referred to as 'sand'), coral, macroalgae, and mixed coral/macroalgae. Seagrass was not included as a benthic category because the meadows present in study bays are sparse, patchy and comprise small-bodied, ephemeral species (e.g. *Halophila* spp.; pers obs MM, RD) that are not visible on satellite imagery (Vanderklift et al. 2016). The four habitat categories, combined with mangroves, represent the dominant benthic habitat types present in the nearshore seascapes of the study region based on expert knowledge of the area and ground truthing. They are also ecologically relevant and commonly used classifications when studying ontogenetic and foraging migrations of fish (Grober-Dunsmore et al. 2008; Berkström et al. 2013; van Lier et al. 2018).

The area (m<sup>2</sup>) and seaward perimeter length (m) of fringing mangrove stands were extracted from shapefiles provided by the Western Australian Department of Biodiversity, Conservation and Attractions (ESRI 2020). Shapefiles of mangrove canopy extent were generated following Murray (2020; see ESM methods for details). Briefly, estimates of mangrove foliage cover from photo orthomosaics (collected using remotely piloted aircraft) were used to calibrate a Normalised Difference Vegetation Index (derived from Sentinel-2, 10 m resolution satellite imagery) resulting in a Vegetation Cover Index from which shapefiles were generated.

The intertidal area of each bay was quantified using the Sentinel-2 Normalized Difference Water Index ( $NDWI = (B03 - B08)/(B03 + B08)$ ; McFeeters 1996). The workflow involved first examining historical tide gauge data that span the Sentinel-2 satellite data archive in order to identify those dates that experienced lowest and highest spring tides that also coincided with day and time (~ 10:30 am local time) of a satellite pass. The NDWI raster image representing the two most extreme low and hightide events were then subtracted with the greatest difference in pixel intensity representing the intertidal zone.

## Fish surveys

### *Diver-operated stereo-video (stereo-DOV)*

Adult fish and benthos were surveyed in January 2021. In each of the study bays, divers completed three 5 m × 30 m transects in each of the major available habitat types (coral reef, macroalgal bed, mangrove fringe, and sand; hereafter referred to as a patch), although not all bays contained all habitat types (Fig. 1). The transects were laid out in succession within a single patch and separated by at least 5 m. Fish assemblages were surveyed using underwater diver-operated stereo-video (stereo-DOV; see ESM for details of stereo-DOV design and calibration). While video-based methods for quantifying fish may underestimate the abundance of cryptic species and juvenile fish, these methods reduce the in-water time required and provide a permanent record that can be reviewed (Holmes et al. 2013). The stereo-DOV transects were swum by an experienced scientific diver at a steady speed of ~0.3 m/s (20 m/min) at a height of ~0.5 m above the benthos and cameras tilted on a slight downward angle (Goetze et al. 2019). To minimise the potential effects of time of day and tide, all surveys were conducted during neap tides, at least two hours after sunrise and at least two hours prior to sunset, when coral and macroalgal sites were inundated to a depth of at least 2 m and mangrove sites to a depth of at least 0.5 m (Kruse et al. 2016).

As divers could not swim within mangroves, surveys were conducted along the perimeter of the mangrove stand. While this method may not capture fish deep within the mangrove forest, the majority of fishes only use the seaward fringe of mangrove habitat (Sheaves et al. 2016; Dunbar et al. 2017). Mangroves could not be sampled at a uniform level of inundation as the timing was constrained by conditions that maximised visibility (i.e. incoming or slack tide and low wind speed). This inconsistency is common in the scientific literature and is unlikely to bias the estimates of the abundance of small-bodied species, which have been shown to enter mangroves within the first 30 min of inundation (Olds et al. 2013; Dunbar et al. 2017). However, some larger taxa may enter intertidal mangrove habitats later in the tidal cycle (Meynecke et al. 2008; Dunbar et al. 2017). Estimates of their abundances may therefore

have been influenced by tidal artefacts and should be interpreted cautiously.

### Video analysis

Video footage was analysed using EventMeasure™ software with all fish identified to the lowest possible taxonomic level (SeaGIS Pty Ltd 2020a). Individuals further than 5 m in front or 2.5 m either side of the stereo-DOV were excluded to maintain a consistent sampling area among sites and habitats.

Estimates of habitat structural complexity were obtained from stereo-DOV footage by a single experienced analyst (Collins et al. 2017). Visual estimates are a commonly used method to quantify structural complexity and are comparable to photogrammetric techniques and in situ measures (Gratwicke and Speight 2005; Wilson et al. 2007; Bayley et al. 2019). Five still images (~6 m apart) were extracted from each video transect and the structural complexity of the substrate was classified on the 0–5 scale of Polunin and Roberts (1993), where 0=no vertical relief, 1=low and sparse relief, 2=low but widespread, 3=moderately complex, 4=very complex with numerous caves and fissures, and 5=exceptionally complex with high coral cover, numerous caves and overhangs.

### Benthic surveys

To quantify the composition of the benthic communities, benthic images were collected on the return pass of the stereo-DOV transects (i.e. across the same three 30 m fish transects in each patch). Digital images were taken every 0.5 m along the transect, from a height of 0.5 m above the substrate ( $n=60$  per transect). Benthic images were analysed using the TransectMeasure™ software and a simplified version of the hierarchical CATAMI classification scheme (Althaus et al. 2015; SeaGIS Pty Ltd 2020b). Fifteen points (based on a preliminary precision analysis) were randomly overlaid on each image and the benthos under each point was classified to the highest resolution possible. The underlying substrate (unconsolidated or consolidated substrate) and the dominant biota (if present; hard coral, soft coral, seagrass, macroalgae, turf algae, mangrove, and sponge) were

classified for each benthic point. Each category was then expressed as percent cover of the transect.

In addition to benthic photo transects, in situ measurements of macroalgal canopy parameters were collected in macroalgal patches, as the height and density of canopy-forming macroalgae can influence the abundance of fish (Wilson et al. 2017). Divers quantified holdfast density and height of canopy forming macroalgae (e.g. *Sargassum* spp.) in six 0.5×0.5 m quadrats located at 5 m intervals along the fish transects.

### Seascape metrics

Locations of fish/benthic transects were overlaid onto the combined benthic habitat map, mangrove extent, and intertidal extent shapefiles to determine the spatial characteristics of the seascape surrounding each transect. Habitat categories included for spatial analysis were coral reef, macroalgae, sand, and mangrove. Mixed coral/macroalgae habitat was excluded from further analyses due to its relative rarity. Because different fish species may respond dissimilarly to their environment due to functional differences in mobility and size, a multi-scale exploratory approach was used to quantify seascape configuration (Wiens et al. 1993; Pittman and McAlpine 2003; Pittman et al. 2007). Initially, buffer zones surrounding each transect were defined at four different spatial scales (100, 200, 300, and 500 m radii) for the calculation of seascape metrics. The minimum buffer size of 100 m was dictated by the resolution of benthic habitat maps while the maximum buffer of 500 m was dictated by the small size of many of the study bays. However, seascape metrics calculated at the 100 m scale did not have a good spread of values due to typically large habitat patch sizes and therefore were excluded from further analyses. Seascape metrics calculated at the 300 m were highly correlated ( $R^2 > 0.8$ ; i.e. redundant variables) to both the 200 and 500 m scales in all instances and were also excluded from further analyses. The remaining 200 and 500 m buffers are at a spatial scale relevant to the reported daily home ranges of many taxa of interest and are commonly used in the seascape ecology literature (Kramer and Chapman 1999; Pittman et al. 2007; Kendall et al. 2011; Green et al. 2015). Buffers were clipped by the shoreline and the 7 m depth contour to ensure only shallow water



habitat that could be confidently digitised from satellite imagery was represented.

The area (m<sup>2</sup>) of coral, macroalgae, and sand habitat, as well as intertidal habitat, within each buffer was calculated and expressed as a proportion of the total area of the clipped buffer (mangrove metrics were calculated separately, see below). Structural connectivity to alternative habitat types (e.g. sand and macroalgae for coral transects) was calculated using the function developed by Hanski (1998) and Moilanen and Nieminen (2002), as described in Berkström et al. (2013). Briefly, the connectivity of a transect to a given habitat type is a function of the sum of areas of the given habitat type within a buffer, weighted by their distance from the target transect (Calabrese and Fagan 2004).

Due to the shape of some bays, the 500 m buffer excluded most or all the mangrove habitat present. Increasing the maximum buffer size was not feasible as buffer size was constrained by the area of each bay within the 7 m contour. Therefore, the areal extent and connectivity to mangroves were calculated at the bay scale, rather than within each buffer (Berkström et al. 2013). A modified connectivity metric (connectivity and availability index; CAI) was used to capture both the structural connectivity to and the variation in temporal availability (i.e. the proportion of time the fringe of an intertidal mangrove stand was accessible to fish) of mangrove habitat for all transects. CAI was calculated as a function of the shortest navigable distance (i.e. not passing over land) from a transect to the edge of mangrove habitat (for mangrove transects this distance was set as 1 m), the length of the seaward perimeter of the mangrove stand, and the proportion of the tidal cycle during which the seaward fringe of the mangrove would be inundated. The length of the seaward perimeter was used in place of the areal extent as several studies have demonstrated that the majority of fish use only the fringe of intertidal mangrove habitat (Sheaves et al. 2016; Dunbar et al. 2017). The proportion of the tidal cycle during which a given mangrove stand was inundated was calculated by first extracting the elevation of the mangrove seaward perimeter at 25 m intervals from the National Intertidal Digital Elevation Model (Bishop-Taylor et al. 2019). A tidal harmonic analysis using UTIDE (Codiga 2011) was then conducted using data from in situ RBRsolo<sup>3</sup> pressure sensors

that had been deployed throughout the archipelago to generate a predicted tide from 2019 to 2021, relative to mean sea level. Finally, the amount of time that the tide was above each elevation point was calculated and summarised to an average value for each site.

Lastly, the Shannon-Wiener evenness index (SEI) of the seascape within the 200 and 500 m buffers was calculated for each transect. This index describes the relative abundance of different patch types in a seascape, incorporating the homogeneity among the seascape elements (Shannon 1948; Simpson 1949; Betzabeth and de los Angeles 2017).

#### Environmental metrics

Environmental data were obtained for each patch using a combination of techniques. The depth of each transect was extracted from high-resolution bathymetry (see ESM for details). Turbidity within the macrotidal waters of the Dampier Archipelago is highly variable over short time periods (e.g. hours–days), therefore satellite-derived KD490 (diffuse attenuation coefficient at 490 nm [KD2 algorithm]) was used as a proxy measure, rather than a one-off in situ measures (Pearce et al. 2003). Daily KD490 data for the five years preceding sampling (January 2016–January 2021) was retrieved from the NOAA ERDDAP data server (dataset ID: erdMH1kd4901day). Average long-term KD490 values were calculated for each site, as the 4 km resolution of this product precluded patch- or transect-level measures. The catchment area of each bay was used as a proxy for potential freshwater and terrigenous sediment input. Catchment area was calculated using SAGA-GIS Module Library Documentation (v2.1.3) in QGIS (Moyroud and Portet 2018). The underlying terrain data was derived from a 1 m resolution airborne light detection and ranging (topoLiDAR) dataset (see McDonald et al. 2020 for more detailed methodology) and LiDAR data gaps were filled using lower resolution SRTM 1 s arc DEM (Wilson et al. 2011). To assess the spatial variability in wave energy, a high-resolution wave model was developed using SWAN (Simulating WAVes Nearshore; Booij, 1999) and significant wave height was extracted for each embayment (see ESM for model validation and simulation details).

All spatial and environmental metrics were calculated using the R Language for Statistical Computing

(hereafter referred to as R; version 4.2.0) and the `sf` (version 1.07), `rredap` (version 1.0.2), `spatialEco` (version 1.3-7) packages (Pebesma 2018; Evans and Murphy 2021; R Core Team 2022; Chamberlain 2023).

### Human use metric

In the absence of any available data on the spatial distribution of recreational fishing pressure in the Dampier Archipelago, potential recreational fishing pressure was quantified for each patch as the distance to the nearest boat ramp. The distance to boat ramp was manually measured as the shortest navigable distance between the nearest boat ramp and the patch using ArcMap 10.8.1 (ESRI 2020). While past work has demonstrated higher abundances of fished species at reefs further from boat ramps, it should be noted that the presence of privately-owned shacks on some of the islands of the Dampier Archipelago may influence the reliability of this metric as a proxy of fishing pressure (Stuart-Smith et al. 2008; Aston et al. 2022). Additionally, although the charter fishing effort in the Dampier Archipelago is relatively low and evenly spread (WA DOF 2015), it is important to note that this metric is unlikely to capture potential impacts of charter fishing operations.

### Data analysis

Analysis of variance (ANOVA) tests were used to confirm whether different habitat types contained distinct fish assemblages. Due to non-normality of residuals, permutational analysis of variance (permutational ANOVA) tests were used to determine whether total abundance and species richness varied between habitats (fixed, four levels) and sites (random, 12 levels, nested within habitat). Data were  $\log(x + 1)$  transformed prior to analysis and converted to a Euclidian distance matrix. Analyses were conducted in PRIMER v7 with PERMANONA+ (Anderson et al. 2008). Significant differences were further investigated using pairwise permutational ANOVAs. A permutational ANOVA test was also used to determine whether taxonomic distinctness of fish assemblages varied between habitats; however, sand transects were excluded as only two transects contained enough unique species. Average taxonomic distinctness is a measure of the average distance between all

pairs of species in a taxonomic tree. This metric captures phenotypic differences and functional richness, is independent of sampling effort, and is insensitive to major habitat differences, allowing for comparisons across habitats (Clarke and Warwick 1998). Average taxonomic distinctness was calculated based on  $\log(x + 1)$  transformed data (to downweight abundant species) using R and the `vegan` package (version 2.6-2; Oksanen et al. 2022; R Core Team 2022).

Fish community composition across habitats and sites was compared using multivariate analyses. Data were  $\log(x + 1)$  transformed and converted into a Bray–Curtis similarity matrix for analysis. A permutational multivariate analysis of variance (PERMANOVA) was then used to test for differences between habitats and sites using the same design as the univariate ANOVA. Significant differences were further investigated using pairwise PERMANOVA. Non-metric multi-dimensional scaling (nMDS) was used to visualise differences in fish assemblages between habitats and sites. Vectors derived from the Bray-Curtis similarity matrix and corresponding to species with significant correlations ( $p < 0.05$  and  $R^2 \geq 0.3$ ) were overlaid onto the nMDS plot using R and the `vegan` package (Oksanen et al. 2022; R Core Team 2022).

Relationships between the suite of potential predictor variables (ESM Table 1) and fish assemblage response metrics (ESM Table 2) were investigated using a full-subsets approach (FSS) and generalised additive mixed models (GAMMs). GAMMs use a sum of smooth functions to model covariate effects, allowing for more flexible functional dependence of the response variable on the covariates, without the requirement for assumptions of the parametric form of the relationship (Wood 2011; Fisher et al. 2018). The FSS approach fits all possible combinations of variables, and calculates the AICc (Akaike information criterion corrected for small sample sizes) for each model (Akaike 1998; Fisher et al. 2018). Models were limited to two explanatory variables to avoid overfitting and difficulty interpreting results. Models containing variables with pairwise correlation coefficients exceeding 0.28 were excluded as even low levels of collinearity between variables can result in inaccurate model parametrisation, decreased power, and exclusion of significant predictor variables (Graham 2003; ESM Fig. 3). Site and Island were included as random effects to increase the inferential

power of the model and to account for overdispersion and correlation (including potential spatial autocorrelation) in the data (Wood 2006; Harrison 2014). Variable importance was determined by summing the weight for all models containing each variable and was used to assess the relative importance of predictor variables (Burnham and Anderson 2002). Models were considered to have similar explanatory power if they were within two AICc units of the model with the lowest AICc, in which case the ‘best’ model(s) were selected based on variable importance and model weight (Akaike 1998). When there was no clear ‘best’ model, the model with the lowest AICc

was presented in Table 1, with the remaining candidate models reported in ESM Table 5. All statistical analyses were conducted using R and the FSSgam (version 1.11), gamm4 (version 0.2-6) and mgcv (version 1.8-40) packages (Wood 2011; Fisher et al. 2018; R Core Team 2022).

Due to significant differences in fish assemblage composition between habitat types, and habitat-specificity of ecologically relevant potential predictor variables, FSS GAMMs were conducted separately for coral, macroalgae, and mangrove habitats. Response variables modelled included total abundance, species richness, average taxonomic distinctness, and the

**Table 1** Best generalised additive mixed models for predicting the total abundance, species richness, average taxonomic distinctness, and abundance of selected fish functional groups

in coral, macroalgae, and mangrove habitats in the Dampier Archipelago, Western Australia

Response variable	R <sup>2</sup>	ΔAICc	wAICc	edf	Best model
<b>Coral</b>					
Total abundance	0.61	0	0.93	8.18	CI sand 200 m + Structural complexity
Species richness	0.6	0	0.15	6.61	Structural complexity
Taxonomic distinctness	0.7	0	0.19	11.5	Structural complexity + PA sand 200 m
Carnivore	0.34	0.79	0.13	5.88	Structural complexity
Corallivore	0.44	0	0.86	8.18	CAI mangrove bay + PA coral 200 m
Herbivore	0.45	0	0.97	10.14	CI macroalgae 500 m + Structural complexity
Micro-invertivore	0.56	0	0.44	9.74	CI macroalgae 200 m + Structural complexity
Planktivore	0.48	0	0.66	7.74	Structural complexity + PA macroalgae 500 m
Scraper	0.39	0	0.84	8.8	CI sand 200 m + % Hard coral
<b>Macroalgae</b>					
Total abundance	0.38	0	0.1	5.94	Depth + % Macroalgae
Species richness	0.55	0	0.51	5.53	Structural complexity + SEI 200 m
Taxonomic distinctness	0.4	0	0.15	5.89	CAI mangrove bay + % Hard coral
Carnivore	0.53	0	0.36	9.58	CAI mangrove bay + % Macroalgae
Herbivore	0.14	0	0.32	10.57	CI coral 500 m + PA macroalgae 500 m
Micro-invertivore	0.45	0	0.38	6.08	KD490 + SEI 200 m
Planktivore	0.21	0	0.51	6.06	CI coral 200 m + KD490
Scraper	0.32	1.59	0.11	5	Structural complexity + PA sand 200 m
<b>Mangrove</b>					
Total abundance	0.23	0	0.1	3	Null model
Species richness	0.36	0	0.07	4.86	CI macroalgae 500 m
Taxonomic distinctness	0.7	0	0.2	6.46	CI coral 200 m + Structural complexity
Carnivore	0.6	0	0.43	4.96	CI macroalgae 500 m
Micro-invertivore	0.14	0	0.46	4.88	CI coral 200 m
Planktivore	0.11	0	0.11	3	Null model

All models within two units of the lowest AICc value are reported in ESM Table 5. Bay, 200 m, and 500 m in seascape variable names indicate scale at which the metric was calculated

ΔAICc Delta Akaike Information Criterion corrected for small sample sizes, wAICc AICc weight, edf estimated degrees of freedom, SEI Shannon-Weiner evenness index, CI connectivity index, PA proportional area, CAI connectivity and availability index

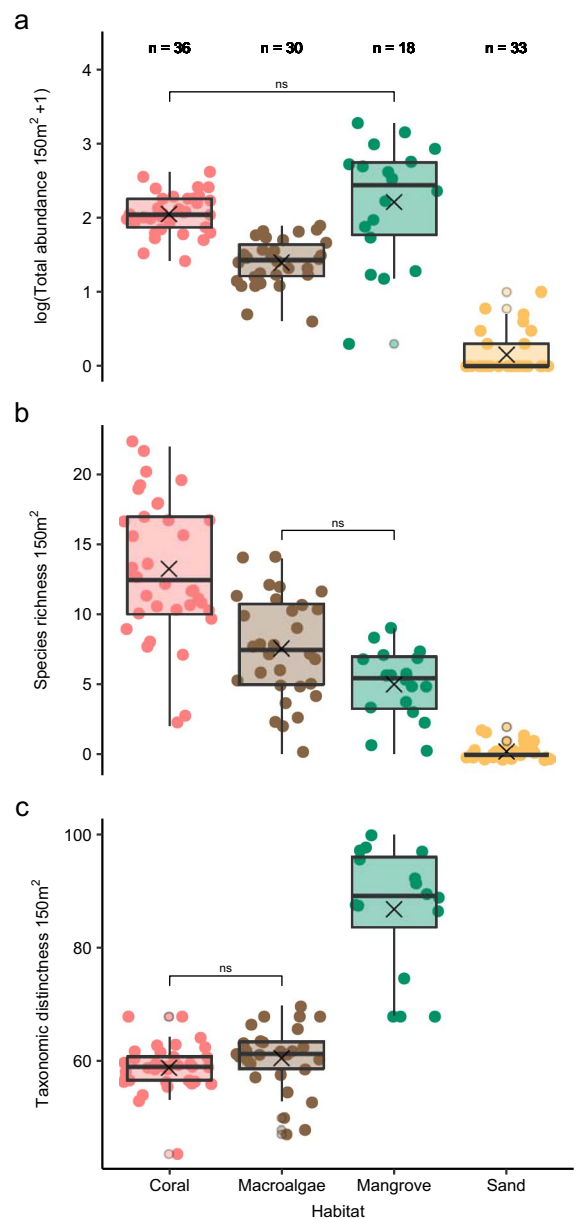
abundance of six common functional groups (present in >20% of transects within a given habitat type; ESM Table 2). Fish species were initially assigned to nine functional groups based on diet and feeding behaviour as reported in the literature and on Fish-Base (see ESM Table 3 for full species list and functional group allocations; Wilson et al. 2008; Pratchett et al. 2011; Froese and Pauly 2022). FSS GAMM analyses were focused on six of the nine assigned functional groups, representing distinct pathways of primary and secondary consumption. Relatively rare functional groups and those dominated by small-bodied cryptic species were excluded (ESM Tables 2 and 3). Supplemental FSS GAMMs were also conducted on the abundances of common genera within each functional group and are presented in the supplementary material (ESM Table 2; ESM Table 6). Response data were not transformed as selecting an appropriate error distribution accounted for non-normal data distribution (see ESM Table 2 for details). A separate set of potential predictors were defined for each habitat type to ensure that only ecologically relevant predictors were included (ESM Table 1). Predictor variables were plotted, assessed for normal distributions and spread of values (as GAMMs are sensitive to the spread of predictors), and transformed or removed from the suite of predictors accordingly prior to analysis (see ESM Table 1 for details).

## Results

### Habitat-specific fish assemblages

The 117 stereo-DOV transects recorded 96 species spanning 61 genera and 35 families (ESM Table 3). The sand habitat contained very low abundances and diversity of fish, and no unique species, and as such was excluded from all further analyses (Fig. 2, ESM Table 3).

The total abundance and species richness of fish assemblages differed significantly among habitat types (Fig. 2, ESM Table 4). Fish abundance in mangrove and coral habitats were similar and both contained significantly more fish than macroalgal habitats (Fig. 2a, ESM Table 4). There was a significant effect of site (nested within habitat) on the total abundance of fish; however, the effect size of site was negligible compared to that of habitat (ESM Table 4).



**Fig. 2** **a** Total abundance ( $\log_{10}(x+1)$  transformed), **b** species richness, and **c** taxonomic distinctness of fish assemblages per 150 m<sup>2</sup> stereo-DOV transect in coral, macroalgae, mangrove, and sand habitats in the Dampier Archipelago, Western Australia. Fish metrics differed significantly among habitats ( $p < 0.05$ ), except those indicated by “ns”. n: number of transects completed in each habitat type. Boxplots indicate quartile values. Mean values are indicated by ‘X’

Mangroves exhibited the greatest variation in total abundance of fish, which was driven by the presence of large schools of bluestripe herring (*Herklotsichthys*

*quadrifasciatus*) and Apogonidae in some transects (Fig. 2a; ESM Table 3). Species richness was significantly higher in coral than in macroalgae and mangrove habitats, with no significant effect of site detected (Fig. 2b, ESM Table 4). Taxonomic distinctness of fish assemblages was highest in mangrove habitats due to the presence of species of Mugilidae (*Myxus elongatus*) and Clupeidae (*H. quadrifasciatus*) which represent orders absent from coral and macroalgal habitats (Fig. 2c; ESM Tables 3 and 4).

The composition of fish assemblages differed significantly between all habitat types (ESM Table 4). There was a significant effect of site (nested within habitat); however, similarly to the univariate assemblage metrics the effect size of habitat was larger than that of site (ESM Table 4). An nMDS plot revealed strong clustering of fish assemblages within habitat types, with little overlap between habitats (Fig. 3). Indeed, habitats contained largely distinct groups of fish species, with 73.5% of observed species recorded in a single habitat type (44.9%, 16.3%, and 11.2% occurring solely in coral, macroalgae, and mangrove habitats, respectively; ESM Table 3). Coral habitats were characterised by higher abundance

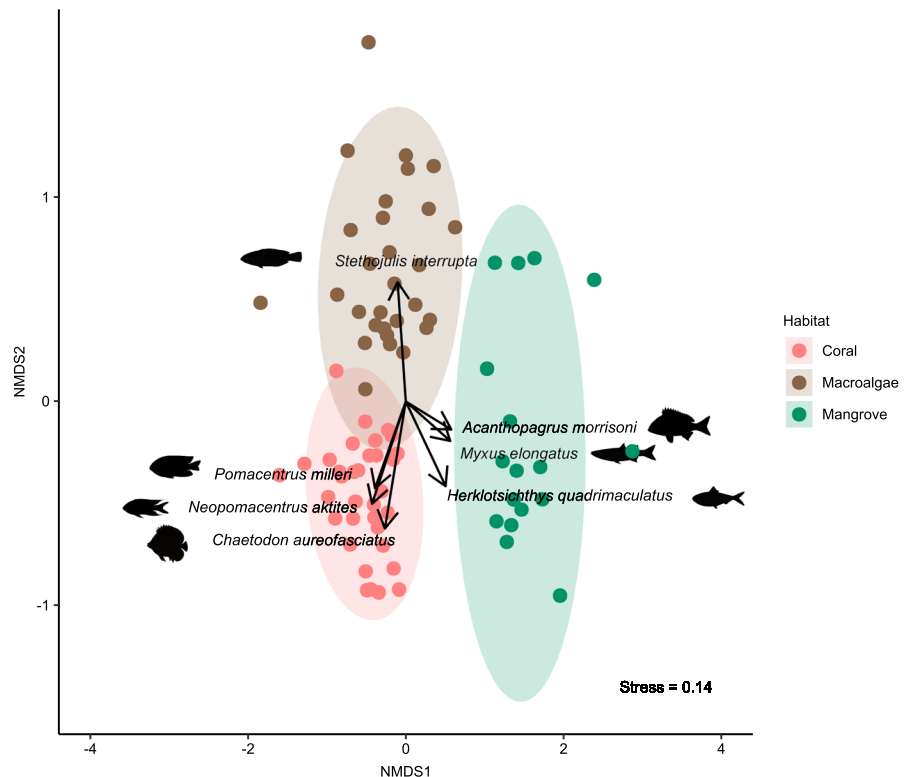
of Pomacentrids (in particular, Western Australian demoiselle [*Neopomacentrus aktites*] and golden butterflyfish [*Chaetodon aureofasciatus*]; Fig. 3). Fish assemblages in macroalgal habitats were more variable than those in coral; however, the brokenline wrasse (*Stethojulis interrupta*) was recorded in most transects. Mangrove assemblages were distinguished by schools of *H. quadrifasciatus*, and the presence of sand mullet (*M. elongatus*) and western yellowfin seabream (*Acanthopagrus morrisoni*; Fig. 3).

As the composition of fish assemblages (and therefore the species composition of several functional groups) differed greatly between habitat types, subsequent analyses investigating the drivers of functional group distribution were conducted separately for each habitat type to account for species-specific responses to structuring forces (Fig. 3; ESM Table 3).

Predictors of total abundance, species richness, taxonomic distinctness, and functional group abundance

The relative importance of local habitat composition and quality, seascape configuration, environmental

**Fig. 3** Non-metric multi-dimensional scaling plot of fish assemblages in coral, macroalgae, and mangrove habitats in the Dampier Archipelago, Western Australia. Significant ( $p < 0.05$ ) species vectors with  $R^2 \geq 0.3$ . Ellipses indicate 95% confidence intervals





◀**Fig. 4** Heat map of predictor variable (x-axis) importance scores from full-subsets generalised additive mixed model analyses relative to coral (pink/top), macroalgae (brown/middle), and mangrove (green/bottom) fish assemblage response variables (y-axis). Predictor variables are categorised (local habitat composition and complexity, seascape configuration, environmental context. *Envt*, and human use *HU*). *C* coral, *MA* macroalgae, *MG* mangrove, *S* sand, *I* intertidal, *SEI* Shannon-Weiner evenness index, *CI* connectivity index, *PA* proportional area, *CAI* connectivity and availability index. Bay, 200 m, and 500 m in seascape variable names indicate scale at which the metric was calculated

conditions, and human use variables differed between various aspects of fish assemblage structure, and between habitats. In coral and macroalgal habitats, measures of overall diversity and abundance were most strongly influenced by local habitat complexity (Fig. 4). Habitat complexity was also an important predictor of abundance for most functional groups in these habitats, with measures of seascape configuration exerting secondary, functional group-specific effects (Fig. 4). The relative importance of environmental metrics was generally low across all models, except for micro-invertivores and planktivores in macroalgal habitats. Similarly, the human use metric was of limited importance except for models of *Epinephelus* spp. abundance (Fig. 4; ESM Fig. 5; ESM Table 6).

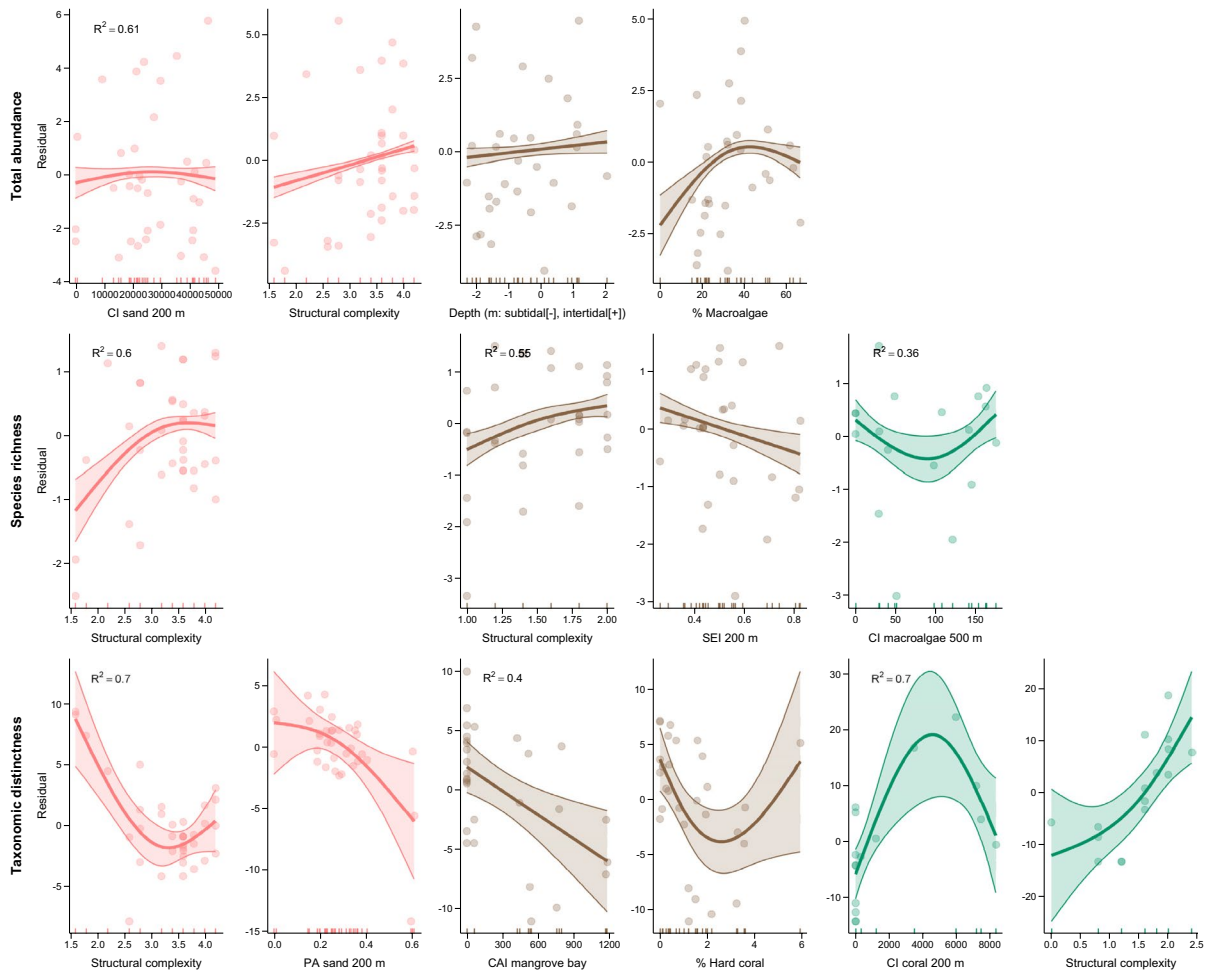
In mangrove habitats, local habitat and environmental metrics had lower average variable importance than seascape metrics (Fig. 4). However, despite their importance, measures of seascape configuration were poor predictors of assemblage- and functional group-level metrics (Figs. 5 and 6). This is likely a consequence of the high variability in abundance and composition of mangrove fish assemblages (Figs. 2 and 3).

### Coral habitats

Structural complexity consistently appeared in the best models explaining spatial variation in the abundance and diversity of fish assemblages on coral reefs (Figs. 4 and 5; Table 1). Higher structural complexity positively influenced both the total abundance and species richness of fish in coral reef habitats, including abundance of four of the six functional groups modelled (carnivore, corallivore, herbivore, micro-invertivore, and planktivore; Figs. 5 and 6). In contrast, the taxonomic distinctness of fish assemblages

in coral habitats was negatively influenced by structural complexity and the proportional area of sand habitat (200 m scale; Fig. 5). Taxonomic distinctness of coral fish assemblages also exhibited a positive relationship with percent cover of unconsolidated substrate, which was strongly negatively correlated with complexity (pairwise correlation coefficient =  $-0.54$ ) and thus does not appear in the same model (Figs. 4 and 5; Table 1; ESM Fig. 4). As local habitat composition becomes more heterogeneous (i.e. contains not only reef and hard coral, but also rubble and sand), the phylogenetic diversity of species observed increases (Fig. 5). This pattern is predominantly driven by the increasing diversity of phylogenetically similar species of Pomacentridae, and to a lesser extent Labridae, present in more complex coral reefs (ESM Table 3). Connectivity to sand habitat at the 200 m scale was an important predictor for the total abundance of fish in coral habitats; however, no directional relationship was apparent (Fig. 5; Table 1). Several other predictor variables appeared in candidate coral species richness models, but none increased model weight (ESM Table 5).

Although seascape metrics were generally weak predictors of overall fish diversity and abundance on coral reefs, connectivity to non-reef habitats had varying and contrasting effects on the abundance of different functional groups. The abundance of herbivores (predominantly Acanthuridae) and planktivores (a range of Pomacentridae, Apogonidae, and Caesionidae) declined with connectivity to and proportional area of macroalgae (respectively) at the 500 m scale, but increased in locations with high structural complexity (Fig. 6). Conversely, micro-invertivores were more abundant on coral reefs with high connectivity to macroalgal habitat, a pattern which was predominantly driven by *Halichoeres* spp. and *Thalassoma* spp. (Fig. 6; ESM Fig. 5, ESM Table 6). Proportional area of focal habitat was only important for corallivores (Chaetodonts), which exhibited a strong positive relationship with coral habitat availability (PA coral; Figs. 4 and 6; Table 1, ESM Table 3). While connectivity to mangroves was also an important predictor for corallivore abundance, no directional relationship was evident (Figs. 4 and 6). The abundance of scrapers (Scarine labrids) in coral habitats peaked with moderate levels of coral cover and with moderate connectivity to sand habitats (Fig. 6).



**Fig. 5** Best generalised additive mixed model residual plots describing total abundance, species richness, and taxonomic distinctness of fish assemblages in coral (pink), macroalgae (brown), and mangrove (green) habitats in the Dampier Archipelago, Western Australia (Table 1). Only models with

$R^2 \geq 0.3$  are presented. *SEI* Shannon-Weiner evenness index, *CI* connectivity index, *PA* proportional area, *CAI* connectivity and availability index. Bay, 200 m, and 500 m in seascape variable names indicate scale at which the metric was calculated

Several variables with low importance scores also appeared in candidate carnivore models (i.e. with  $\Delta AICc$  values  $< 2$ ; ESM Table 3). Candidate models of carnivore abundance included distance to boat ramp (positive correlation), percent cover of turf algae (positive correlation), connectivity to mangroves (no directional pattern), and connectivity to sand at the 500 m scale (no directional pattern; ESM Fig. 4, ESM Table 5). This broad range of candidate models reflects the taxonomic diversity of the carnivore functional group (38 species from 15 families; ESM Table 3). For example, *Lutjanus* spp. were most strongly influenced by structural complexity,

while *Epinepheulus* spp. were positively correlated with distance from a boat ramp (ESM Fig. 5, ESM Table 6).

#### Macroalgal habitats

Both percent cover of macroalgae and structural complexity were important predictors of fish diversity and abundance in macroalgal habitats (Fig. 4). Macroalgal beds with higher complexity exhibited greater fish diversity and overall abundance, as well as greater abundance of carnivores and scrapers (Figs. 5 and 6; Table 1). Species richness was also



weakly negatively related to seascape heterogeneity at the 200 m scale; however, the importance score of this variable was relatively low (Figs. 4 and 5). Total abundance of fish was positively correlated to percent cover of macroalgae (and consequently structural complexity; pairwise correlation coefficient = 0.74; Fig. 4, ESM Fig. 3, ESM Table 5). Overall fish abundance was also somewhat higher in shallower macroalgal beds (Fig. 5). Other variables present in the total abundance candidate models had low importance scores and did not increase the weight of the model (Fig. 4, ESM Table 5). Taxonomic distinctness of macroalgal fish assemblages declined at moderate levels of hard coral cover and with increasing connectivity to mangrove habitat (Fig. 5; Table 1).

Several measures of seascape configuration were included in the best models for the abundance of functional groups in macroalgal habitats; however, these metrics were generally weaker predictors than local habitat measures. In addition to a positive relationship with complexity, scraper abundance increased with the proportional area of sand in the seascape (200 m scale; Fig. 6; Table 1). Similarly, connectivity to mangrove habitat appeared in the best model of carnivore abundance, in addition to macroalgal cover; however, no directional relationship was evident (Fig. 6). Within the carnivore group, in addition to a positive relationship with macroalgal cover, the abundance of *Lethrinus* spp. and *Lutjanus* spp. were negatively correlated with proportion of sand in the seascape and seascape heterogeneity (both at the 200 m scale), respectively (ESM Fig. 5; ESM Table 6).

Micro-invertivores were the only functional group to respond to environmental metrics, with their abundance increasing at higher levels of turbidity (KD490) and decreasing in more heterogeneous seascapes (200 m scale) in macroalgal habitats (Figs. 4 and 6; Table 1). The alternative candidate micro-invertivore model also showed a positive relationship with significant wave height (ESM Fig. 5, ESM Table 6).

### Mangrove habitats

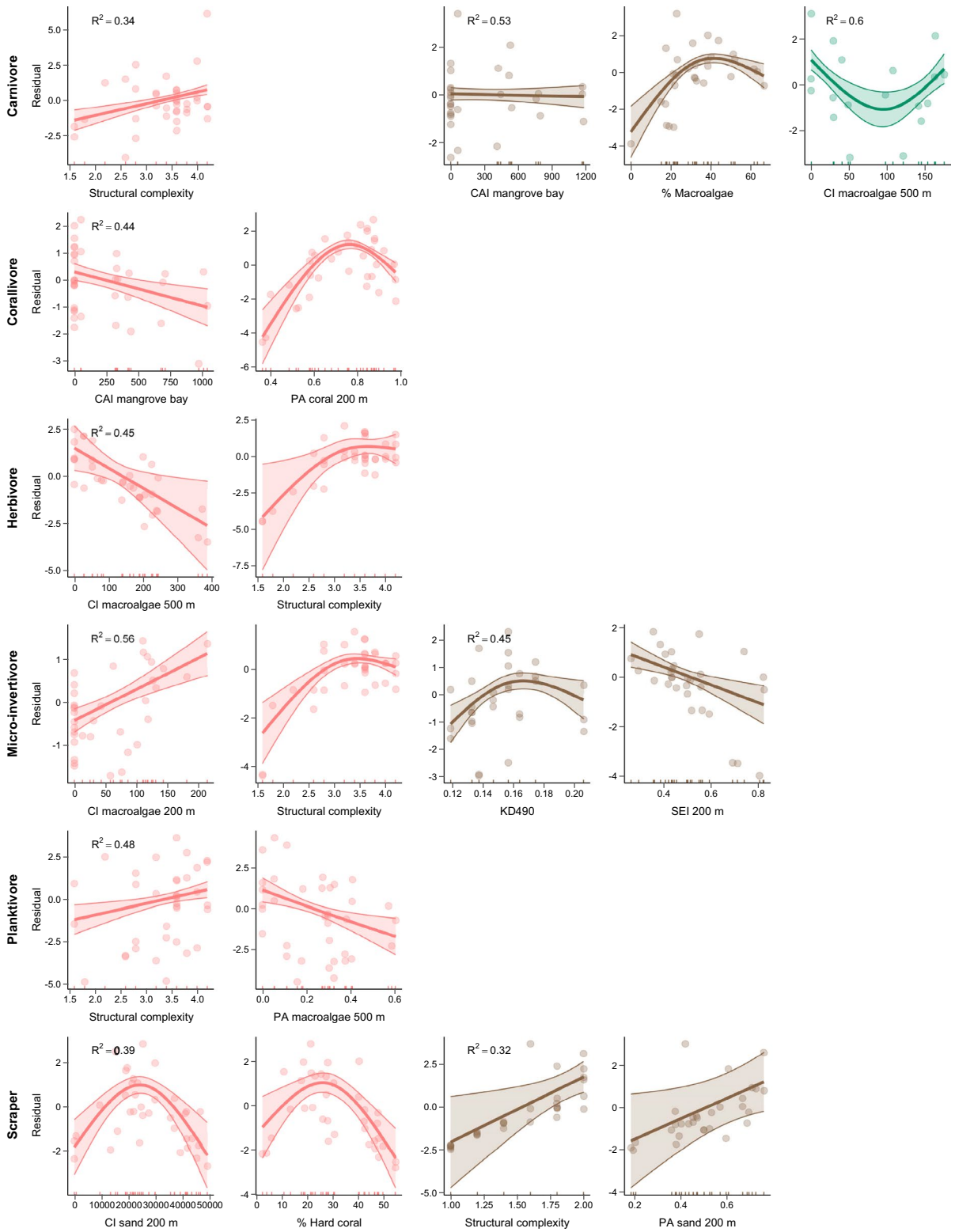
The total abundance of fish in mangrove habitats was highly variable and was not related to any of the predictor variables (i.e. the best model was the null; Fig. 2; Table 1). Similarly, while numerous predictor

variables appeared in candidate models of mangrove species richness, none (including the ‘best’ model) had high variable importance scores or model weights (Fig. 4, ESM Table 5). Consequently, only a weak pattern of declining species richness at intermediate levels of connectivity to macroalgal habitats (500 m scale) was observed for mangrove fish assemblages (Fig. 5). In contrast to the patterns observed in coral habitats, the taxonomic distinctness of mangrove fish assemblages increased with structural complexity (Fig. 5; Table 1). Connectivity to coral habitats at the 200 m scale was also an important variable for the taxonomic distinctness of mangrove fish assemblages; however, this pattern was driven by a small number of transects (Figs. 4 and 5).

The abundance of fish within each functional group was also highly variable in mangrove habitats. Consequently, none of the predictor variables were strongly correlated to the abundance of any functional group (Table 1). Connectivity to macroalgal habitat at the 500 m scale was the most important predictor of carnivore abundance with abundance declining at intermediate levels of connectivity (Figs. 4 and 6). Within the carnivore group, the abundance of *Acanthopagrus* spp. and *Choerodon* spp. exhibited strong negative correlations with proportional area of macroalgae and sand habitat, respectively (500 m scale; ESM Fig. 5, ESM Table 6). The remaining general-level models and the micro-invertivore model had low explanatory power ( $R^2=0.14$ ) and the best model for planktivores was the null (Table 1; ESM Table 5).

### Discussion

In this study we investigated the importance of different structuring forces in determining the abundance, diversity, and functional composition of fish assemblages across multiple habitats within the dynamic seascape of the Dampier Archipelago, Western Australia. We found that local habitat composition and complexity were generally better predictors of overall fish abundance and diversity in both coral and macroalgal habitats than seascape configuration or environmental conditions. These findings contrast with previous studies that reported overriding effects of seascape configuration in structuring fish assemblages (Pittman et al. 2007; Olds et al. 2012a; Gilby et al. 2016; Sievers et al. 2020). Rather, our findings



**◀Fig. 6** Best generalised additive mixed model residual plots describing the abundance of fish in six functional groups (carnivores, corallivores, herbivores, micro-invertivores, planktivores, and scrapers) in coral (pink), macroalgae (brown), and mangrove (green) habitats in the Dampier Archipelago, Western Australia (Table 1). *SEI* Shannon-Weiner evenness index, *CI* connectivity index, *PA* proportional area, *CAI* connectivity and availability index Only models with  $R^2 \geq 0.3$  are presented. Bay, 200 m, and 500 m in seascape variable names indicate scale at which the metric was calculated

align with those of van Lier et al. (2018), who found that local habitat condition had the strongest influence on macroalgal fish assemblages, while seascape effects played a secondary role. We also identified distinct fish assemblages associated with specific habitats within the seascape (excepting sand habitats which harboured few fish) and found that the importance of biophysical drivers for fish varied between habitat types and functional groups. These findings contribute to a more nuanced understanding of the role of seascape configuration in structuring fish assemblages. Our results emphasise the importance of local structural complexity for fish and suggest that the value of structural connectivity between habitats depends on environmental context (Boström et al. 2011; Igulu et al. 2014; Bradley et al. 2021).

High structural complexity on coral reefs facilitates diverse and productive fish communities by creating numerous microhabitats and mediating ecological interactions (Hixon and Beets 1993; Graham and Nash 2013; Rogers et al. 2014). Our results demonstrate that structural complexity remains a crucial factor in shaping fish assemblages, even when the influence of seascape, environmental, and human use factors are taken into consideration. Structural complexity emerged as the strongest predictor of coral reef fish assemblages, with higher complexity resulting in increased total abundance, species richness, and representation of carnivores, herbivores, micro-invertivores, and planktivores. This is in contrast to previous studies that found that seascape configuration had a similar or greater effect on fish assemblages compared to structural complexity (Grober-Dunsmore et al. 2008; Olds et al. 2012a; Sievers et al. 2020). The dominance of structural complexity found in our study may be due to the small body sizes and limited home ranges of many of the abundant species recorded (Alvarez-Filip et al. 2011; Green et al. 2015; Nash et al. 2015). Some of these species likely recruit

directly to coral reefs and occupy these habitats throughout their post-settlement life (Wilson et al. 2010; Coker et al. 2014), meaning that any influence of seascape configuration is likely to be overshadowed by variation in local habitat composition and complexity. Additionally, complex habitats may serve as hydrodynamic refuges for small-bodied species in macrotidal systems like the Dampier Archipelago (Johansen et al. 2008; Caldwell and Gergel 2013; Eggertsen et al. 2016). The importance of complexity in this system likely also explains the paucity of fish observed in sand habitats. However, our results also indicated that fish assemblages become taxonomically homogenous in uniformly complex coral reef habitats, highlighting the importance of local habitat heterogeneity to phylogenetic diversity. The relationship between complexity and the abundance of key functional groups underscores the crucial role of reef complexity in regulating benthic community structure, facilitating energy flow, and enhancing resilience (Hughes et al. 2007; Rogers et al. 2014; Graham et al. 2015).

Tropical macrophyte habitats (e.g. mangroves, seagrass, and macroalgae) have been shown to serve as nurseries for certain coral reef fish species (Dorenbosch et al. 2004; Mumby et al. 2004; Lefcheck et al. 2019). Accordingly, numerous studies have reported higher abundance of ‘nursery species’ (i.e. species that occupy macrophyte habitats as juveniles and coral reefs as adults) on coral reefs located near seagrass or mangrove habitats (Mumby et al. 2004; Grober-Dunsmore et al. 2007; Olds et al. 2012a; Harborne et al. 2016; Berkström et al. 2020). However, we found limited evidence that connectivity to mangrove or macroalgal habitat increased abundance or diversity of fishes on coral reefs (except for micro-invertivores). This result is unexpected as several studies in north-western Australia have previously identified macroalgae beds as nurseries for some Siganidae and Lethrinidae species (Wilson et al. 2010, 2018; Evans et al. 2014). The minimal influence of connectivity to potential nursery habitats on coral reef fish assemblages may be attributable to variations in environmental conditions, differences in the quantity/quality/arrangement of habitats, tidal amplitude, or assemblage composition among regions (Kendall et al. 2011; Hemingson and Bellwood 2020). For example, studies that reported benefits of connectivity to mangrove habitat were conducted in systems

with extensive mangrove stands that are regularly inundated by tidal waters (Nagelkerken et al. 2008; Olds et al. 2012a; Berkström et al. 2020). In contrast, mangroves on the islands of the Dampier Archipelago tend to be relatively small, fringing stands, some of which are only inundated for short periods during the day (Semeniuk and Wurm 1987). As such, larger tidal ranges may reduce the value of intertidal mangrove habitat for fish (Barnes et al. 2012; Igulu et al. 2014; Sievers et al. 2020; Bradley et al. 2021), and/or strong tidal currents may facilitate fish migrations over greater spatial scales than in microtidal regions (Gibson 2003; Krumme 2009). Accordingly, inter-habitat migrations may occur over greater scales than those assessed in our study, as has been reported in the Caribbean (e.g. up to 4 km by Nagelkerken et al. 2017). Finally, the composition of fish assemblages may also influence the degree of ontogenetic multihabitat use. Hemingson and Bellwood (2020) reported lower ontogenetic connectivity on the Great Barrier Reef, Australia than in the Caribbean, attributing this difference to the larger adult body size of species comprising the Caribbean assemblages. Techniques such as tagging, telemetry and stable isotopes may be useful to determine the causes of this regional variation in the extent of seascape use by fish.

The complexity of macroalgal habitats is a function of both the rugosity of the underlying substrate and the soft macroalgal canopy structure (Wilson et al. 2014; van Lier et al. 2017). Our results showed that, similar to coral habitats, habitat complexity of the underlying reef was the best predictor of the overall abundance and diversity of fish in macroalgal habitats, whilst canopy height and density were relatively poor predictors. These results imply that when reef structure is moderately high, the benefits of structure associated with canopy become less important. Nonetheless, macroalgae cover was still an important predictor of fish abundance as complex macroalgae beds may offer food resources in the form of additional macroalgae biomass, epiphytic algae, juvenile fishes, and increased productivity of invertebrate epifauna (Tebbett et al. 2020; Fulton et al. 2020; Chen et al. 2021). Indeed, we observed an increased abundance of generalist carnivores (specifically Lethrinidae and Lutjanidae species) in more complex macroalgal beds. Interestingly, we did not see a similar positive correlation between micro-invertivore abundance and macroalgal cover. This may be a result of the feeding

behaviour of the two dominant micro-invertivore genera observed, *Stethojulis* and *Halichoeres*, which tend to forage over the unvegetated components of macroalgal habitats and presumably use the macroalgal canopy primarily for shelter (Chen et al. 2022).

Given the dynamic nature of tropical macroalgal beds, it has been suggested that mobile, canopy-affiliated taxa may migrate to nearby alternative structured habitats during periods of low canopy biomass (Chen et al. 2022). However, we found connectivity to coral or mangrove habitats generally had little influence on the abundance or diversity of fish inhabiting macroalgal beds. This result has two plausible explanations: firstly, the strong currents in macrotidal environments may limit fish movement between habitats (Caldwell and Gergel 2013). Alternatively, these currents may instead facilitate fish movement, expanding fish home ranges beyond the scope of this study and allowing fish to access a wider variety of foraging sites (Krumme 2009). In contrast to previous studies conducted in macroalgae beds (van Lier et al. 2018) and seagrass meadows (Staveley et al. 2017), we observed lower abundance and diversity of micro-invertivores (and consequently overall species richness) in macroalgal beds within more heterogeneous seascapes. This inverse relationship between seascape heterogeneity and macroalgal micro-invertivore abundance may be explained by higher predation risk associated with an increased number of patch edges in more heterogeneous seascapes (Smith et al. 2010). This notion is supported by the positive relationship between micro-invertivore abundance and increased turbidity, as high turbidity may reduce prey detection by visual predators (Gregory and Levings 1998; Utne-Palm 2004). Alternatively, some micro-invertivores may be greater macroalgal specialists than previously thought and thus have limited ability to exploit more heterogeneous seascapes (Fulton et al. 2020). As micro-invertivores are important conduits for the flow of benthic production to higher trophic levels, the mechanisms underlying their varying responses to seascape configuration warrant further investigation (Newcombe and Taylor 2010; Chen et al. 2022).

The mangrove fish assemblages surveyed in the present study contained unique species and, at times, notably high densities of fish. The species assemblages observed in mangrove habitat showed little overlap with those in coral or macroalgal habitats, and as such make a unique contribution to the

overall diversity of the seascape. Similarly distinct fish assemblages have been reported elsewhere in Australia (Barnes et al. 2012; Hemingson and Bellwood 2020), the broader Indo-Pacific (Unsworth et al. 2009), and the Red Sea (Dunne et al. 2023). In contrast, fish assemblages in coral and mangrove habitats in the Caribbean frequently show considerable overlap (Chittaro et al. 2005; Verweij et al. 2006). The interaction between mangrove and coral habitats in the Indo-Pacific appears to be more variable (e.g. Unsworth et al. 2008, 2009), and often weaker, than in the Caribbean (Hemingson and Bellwood 2020), likely due to differences in geomorphology, tidal amplitude, environmental context, and evolutionary history (Barnes et al. 2012; Castellanos-Galindo et al. 2013; Igulu et al. 2014; Berkström et al. 2020; Bradley et al. 2020). Our findings suggest that the predation risk and/or energetic cost of tidal migrations from mangroves to subtidal biotic habitats is prohibitive for fish within the environmental and seascape context of The Dampier Archipelago (Dahlgren and Eggleston 2000; Sheaves 2005). Residual pools of water within the mangroves or rock habitats along the landward edges of bays may instead act as low tide refugia for fish occupying mangrove habitats (Espadero et al. 2021). Further research is required to determine the degree to which mangroves are connected to the broader seascape in macrotidal systems, and to understand the mechanisms dictating the degree of faunal inter-habitat connectivity (Sheaves 2005; Unsworth et al. 2008).

Recreational fishing can have considerable impacts on the biomass and composition of fish assemblages (McPhee et al. 2002; Zuercher et al. 2023). Indeed, previous studies have reported higher abundances of fished species at reefs located further from boat ramps (Stuart-Smith et al. 2008; Aston et al. 2022). While lower abundances of *Ephinephelus* spp. were recorded on coral reefs closer to boat ramps in this study, the same pattern was not evident for other commonly targeted genera (e.g. *Lethrinus*, *Choerodon*, and *Lutjanus*). The limited effects of human use in this study may be due to the dominance of biophysical drivers in shaping fish distributions within the challenging environmental context of the Dampier Archipelago (Fidler et al. 2021). However, it is also possible that distance to boat ramp does not accurately represent recreational fishing pressure in the region. High-resolution data quantifying the spatial

distribution of fishing effort and catch rates would be beneficial in disentangling human impacts from habitat and seascape effects.

This study assessed the relative importance of a wide range of biophysical variables spanning several spatial scales for structuring fish assemblages across multiple habitat types in a tropical seascape. Using this novel framework, we demonstrated that the abundance, diversity, and composition of fish assemblages in the Dampier Archipelago were best predicted by local habitat composition and complexity, rather than measures of seascape configuration or environmental conditions. In contrast with previous work, proximity to potential macrophyte nursery habitats appeared to have little effect on coral reef fish abundance or diversity, except for micro-invertivores. This does not however discount the possibility that mangroves and macroalgae beds serve as nursery habitats in this region. Indeed, as video-based survey methods can underestimate the abundance of juvenile fish (Holmes et al. 2013), these findings may not fully reflect the relative importance of biophysical drivers for juvenile fish, which have limited mobility and are more vulnerable to predation than adults (Dahlgren and Eggleston 2000; Caldwell and Gergel 2013; Green et al. 2015). Future work could consider using complementary sampling methods, such as underwater visual census or eDNA, to further explore how the influence of structuring forces varies between life history stages. Our surveys also indicated that coral, macroalgal, and mangrove habitats contained unique fish assemblages and contributed to the overall diversity of fish within the seascape. Amid growing calls for the consideration of connectivity in marine reserve design, these findings underscore the importance of a deeper understanding of the mechanisms behind regional variation in the effects of seascape configuration on fish (Martin et al. 2015; Olds et al. 2016; Goetze et al. 2021). Our results provide support for management approaches that incorporate the full range of habitats present within tropical seascapes, and prioritise the preservation of structural complexity (Harborne et al. 2017; Sambrook et al. 2019; Wilson et al. 2022). Whilst comprehensive ecological and environmental datasets may not always be available, where such data do exist they can provide valuable insights for marine spatial planning. Given that conservation initiatives often require trade-offs between management objectives (McShane et al. 2011), approaches such as those

used in this study can identify the combinations of local habitat and landscape characteristics that best support specific management goals (e.g. maintaining diversity or specific ecological processes). Furthermore, deepening our understanding of the mechanisms underpinning regional variation in the effects of key biophysical drivers will support the development of tailored strategies for preserving ecosystem function across tropical seascapes.

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**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Competing interests** The authors declare no competing interests. The authors have no relevant financial or non-financial interests to disclose.

**Ethical approval** This research was conducted in accordance with the Department of Biodiversity, Conservation and Attractions animal ethics permit 2020-16 A.

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